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Inhibition of Seagrass Photosynthesis by Ultraviolet-B Radiation[1]

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ROBERT P. TROCINE[2], JOHN D. RICE[3], AND GARY N. WELLS[4]
Department of Biology, Florida Institute of Technology, Melbourne, Florida 32901

ABSTRACT

Effects of ultraviolet-B radiation on the photosynthesis of seagrasses (*Halophila engelmanni* Aschers, *Halodule wrightii* Aschers, and *Syringodium filiforme* Kütz) were examined. The intrinsic tolerance of each seagrass to ultraviolet-B, the presence and effectiveness of photorepair mechanisms to ultraviolet-B-induced photosynthetic inhibition, and the role of epiphytic growth as a shield from ultraviolet-B were investigated.

***Halodule* was found to possess the greatest photosynthetic tolerance for ultraviolet-B. Photosynthesis in *Syringodium* was slightly more sensitive to ultraviolet-B while *Halophila* showed relatively little photosynthetic tolerance. Evidence for a photorepair mechanism was found only in *Halodule*. This mechanism effectively attenuated photosynthetic inhibition induced by ultraviolet-B dose rates and dosages in excess of natural conditions. *Syringodium* appeared to rely primarily on a thick epidermal cell layer to reduce photosynthetic damage. *Halophila* seemed to have no morphological or photorepair capabilities to deal with ultraviolet-B. This species appeared to rely on epiphytic and detrital shielding and the shade provided by other seagrasses to reduce ultraviolet-B irradiation to tolerable levels. The presence of epiphytes on leaf surfaces was found to reduce the extent of photosynthetic inhibition from ultraviolet-B exposure in all species.**

Observations obtained in this study seem to suggest the possibility of anthocyanin and/or other flavonoid synthesis as an adaptation to long term ultraviolet-B irradiation by these species. In addition, *Halophila* appears to obtain an increased photosynthetic tolerance to ultraviolet-B as an indirect benefit of chloroplast clumping to avoid photo-oxidation by intense levels of photosynthetically active radiation.

The threat of a reduction in the stratospheric ozone layer by anthropogenic agents (7, 17, 19, 27), and the concomitant increase in UV radiation reaching the earth's surface (8) has stimulated a renewed interest in the biological effects of UV radiation between 290 and 320 nm (UV-B). Recently, UV-B irradiation has been shown effective in inhibiting leaf expansion (22, 29, 30), seedling growth (1, 21), dark respiration (29), and ion transport (1), as well as altering membrane permeability (9–11). Ultraviolet-B radiation has also been shown to be a potent inhibitor of photosynthesis (4, 5, 16, 26, 29, 30, 35) and a number of partial reactions of phytosynthesis, including Chl synthesis (2, 14), the Hill reaction (2, 5, 14), and electron transport (5, 24, 25).

The objective of this study was to examine the influence of ambient and enhanced UV-B irradiation on photosynthesis in three marine angiosperms: *Halodule wrightii, Syringodium filiforme,* and *Halophila engelmannii.* The photorepair capabilities of the three seagrasses and the role of epiphytes as a shield from increased levels of UV-B irradiation were evaluated.

These three seagrasses were selected for study because of their sensitivity to UV-B irradiation, their distribution along a natural gradient of UV-B and visible radiation intensities, and because of their ecological importance in shallow marine and estuarine systems in terms of total productivity and species diversity. A significant reduction in abundance of these seagrasses or their relocation to deeper waters as a result of increased UV-B levels may have a profound effect on many trophic levels.

MATERIALS AND METHODS

Plant Material and Water Analysis. Intact samples of *H. wrightii* Aschers, *S. filiforme* Kütz, and *H. engelmannii* Aschers, were collected daily from the Indian River lagoonal system (near Melbourne, FL) and transported to the laboratory. Samples of leaf tissue (approximately 75 mg) were excised, cleaned of epiphytes, fresh weights determined, and placed in Petri plates containing FSSW[5] in preparation for irradiation. Fresh seawater was filter sterilized by first passing it through Whatman No. 4 paper followed by Millipore filtrration (0.45 μm). The bicarbonate concentration was determined according to Strickland and Parsons (34) and salinity determined by refractive index.

Irradiation of Tissue. Leaf tissues were irradiated at room temperature (21–25 C) with simulated solar UV-B (290–315 nm) from six FS-40 sunlamps (Westinghouse) filtered by Kodacel TA-401 (5 mil, Eastman Kodak) plastic film. Kodacel effectively absorbs radiation of wavelengths less than 290 nm, eliminating the UV-C component of the sunlamps. The spectral irradiance from this lamp system is shown in Figure 1. Two sets of control tissues were prepared with each experiment. Irradiation controls, screened with Mylar Type-A film (10 mil, Dupont) to remove UV-B, were irradiated simultaneously with the experimental tissues. In addition, as neither Kodacel nor Mylar remove UV-A (315–380 nm), dark controls receiving neither UV-A nor UV-B were prepared and used to correct for any contribution to photosynthetic inhibition by UV-A on the assumption the effects of UV-A (if any) and UV-B were additive in terms of photosynthetic carbon fixation. The effects of UV-A on seagrass photosynthesis are detailed in a paper currently in preparation. To accomplish this correction a Sunburn Ultraviolet Meter (Solar Light Co.) was recalibrated to quantify UV-A and UV-B spectral components as produced by the FS-40 sunlamps. The spectral sensitivity of the Sunburn Ultraviolet Meter is seen in Figure 1.

As the FS-40 sunlamp spectrum does not match the solar

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[2] Present address: Department of Oceanography, Florida Institute of Technology, Melbourne, FL 32901.

[3] Present address: Institute of Food and Agricultural Sciences Agricultural Research and Education Center, P.O. Box 1088, Lake Alfred, FL 33850.

[4] To whom all correspondence should be addressed.

[5] Abbreviations: FSSW, filtered sterilized seawater; PAR, photosynthetically active radiation; SEM, scanning electron microscopy: PI, photosynthetic inhibition.

spectrum exactly (Fig. 1) and not all wavelengths of UV are equally effective at inhibiting photosynthesis, the relative biological efficiency of the radiation environment was determined. The photoinhibition action spectrum of Jones and Kok (20) as normalized by Smith *et al.* (32) was selected as the most appropriate weighting system for calculation of biologically effective irradiance, weighting both UV-B and UV-A (although only UV-B is considered in this paper). The resultant weighted irradiance (UV-B_{PI}) takes into account the wavelength dependency of photosynthetic inhibition. Dosimetry of UV-B_{PI} was controlled by adjusting the lamp to tissue distance and length of exposure (Fig. 2). Biologically effective dose rates and total doses are presented as $(w \cdot m^{-2})_{PI}$ and $(kJ \cdot m^{-1})_{PI}$. Both Kodacel and Mylar films were changed after 40 h of use. A black, absorptive background prevented reflection from the sample platform.

Photorepair treatments consisted of exposing seagrass leaves to UV-B and visible irradiations simultaneously. Visible radiation was provided by six 300-w incandescent lamps adjusted to a PAR intensity of 700 $\mu E\ m^{-2}\ s^{-1}$ between 400 and 700 nm at the leaf surface. A cosine-corrected, λ quantum sensor and meter were used to measure PAR.

Penetration of natural UV radiation through the water column was determined by utilizing the Sunburn Ultraviolet Meter enclosed in a water-proof plastic (polyethylene) housing. Ultraviolet measurements at the mean leaf depth of the seagrasses (30–60 cm) usually ranged between 20% to 50% of the surface fluence rate depending on water depth, water quality and time of year. All underwater UV values reported are from July and August when UV fluence is at its maximum. To interpret the environmental data correctly, several considerations must be made. First, the lack of precise spectral differentiation by the Sunburn Ultraviolet Meter (UV-B *versus* UV-A) resulted in environmental data which

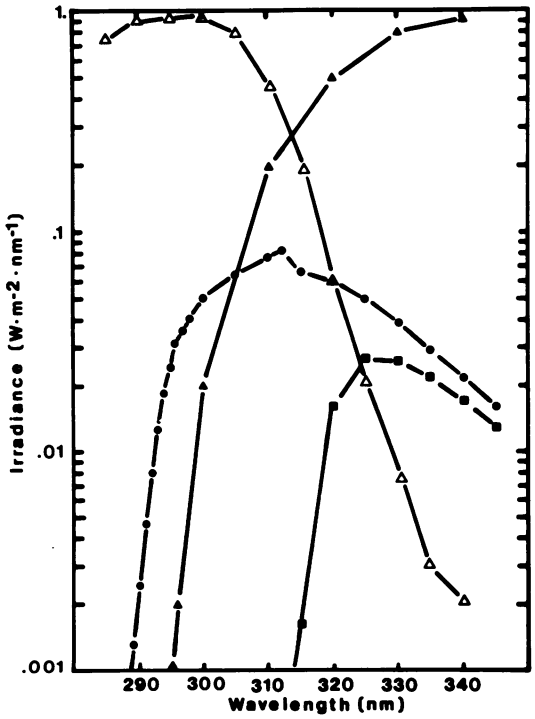

FIG. 1. Spectral irradiance of Westinghouse FS-40 sunlamps and sensitivity of the Sunburn Ultraviolet Meter. Transmission of FS-40 irradiance through Kodacel TA-401, 5 mil (●——●). Transmission of FS-40 irradiance through Mylar Type-A, 10 mil (■——■). Spectral response of the Sunburn Ultraviolet Meter (△——△) (courtesy of Solar Light Co.). Relative global radiation (sun and sky), 20° Zenith angle (▲——▲) (courtesy of Solar Light Co.).

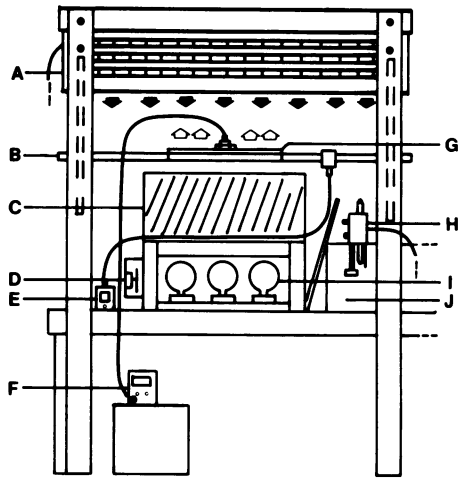

FIG. 2. UV and PAR irradiation apparatus. (A) FS-40 fluorescent sun lamps; (B) adjustable test platform; (C) heat sink; (D) fan; (E) Sunburn Ultraviolet Meter; (F) LICOR light meter; (G) Plexiglas window; (H) water pump; (I) PAR light bank; (J) colling tank.

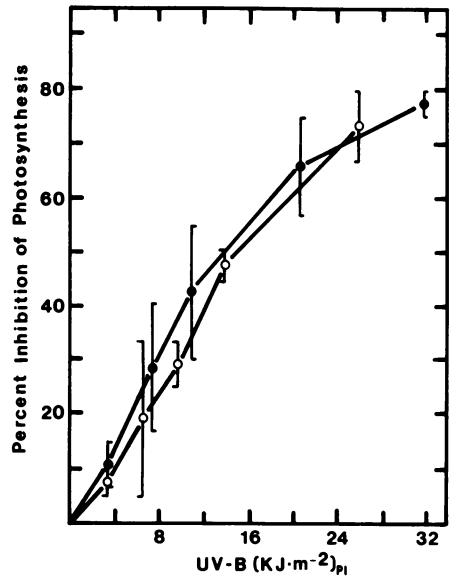

FIG. 3. Per cent inhibition of photosynthesis in *H. engelmannii* by UV-B and the effect of PAR irradiance on UV-B-induced photosynthetic inhibition. Dose rates for UV-B irradiation in the absence of PAR (●——●) ranged from 0.37 to 1.4 $w \cdot m^{-2}_{PI}$. Dose rates for UV-B irradiation in the presence of 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR (○——○) ranged from 0.42 to 1.2 $w \cdot m^{-2}_{PI}$. Zero % inhibition averaged 77.9 ± 24.7 μmol $CO_2 \cdot$mg $Chl^{-1} \cdot h^{-1}$. For experimental conditions, see "Materials and Methods." Vertical bars represent ± one standard error and each value is the mean of eight replicates.

is an amalgam of both. This combined with the relative abundance of UV-A compared to UV-B in sunlight, underwater spectral changes (40), and the reduced biological effectiveness of UV-A in contrast to UV-B (32) result in a slight overestimation in the biologically effective UV-B radiation present. The environmental levels of UV-B_{PI} reported must be considered somewhat greater than actual levels and laboratory reproduction of these values more inhibitory than their solar equivalent.

Photosynthetic Carbon Fixation. After irradiation, the rate of photosynthesis by leaf tissue sections was measured according to the modified procedure of Bassham and Calvin (3) using a PAR of 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the leaf surface and a temperature of 30 C. These parameters were selected from preliminary studies to deter-

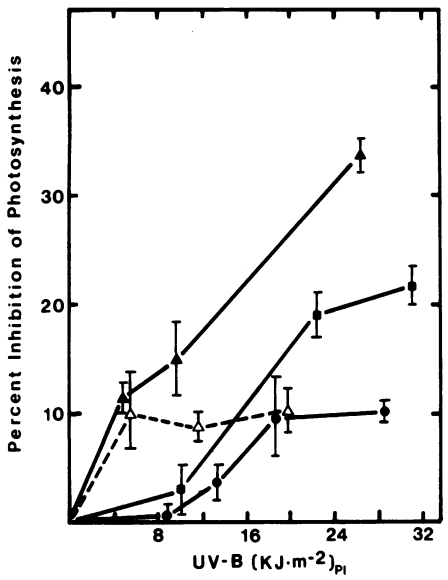

FIG. 4. Per cent inhibition of photosynthesis in *H. wrightii* by UV-B and the effect of PAR irradiance on UV-B-induced photosynthetic inhibition. Per cent inhibition values were plotted on the basis of equivalent dose rates. Dose rates for UV-B irradiation in the absence of PAR ranged as follows: from 0.37 to 0.51 $w \cdot m^{-2}_{PI}$ (●——●); from 0.74 to 0.97 $w \cdot m^{-2}_{PI}$ (■——■); from 1.1 to 1.2 $w \cdot m^{-2}_{PI}$ (▲——▲). Dose rates for UV-B irradiation in the presence of 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR (△- - -△) ranged from 0.4 to 0.97 $w \cdot m^{-2}_{PI}$. Zero % inhibition averaged 75.5 ± 13.6 μmol $CO_2 \cdot mg\ Chl^{-1} \cdot h^{-1}$. Vertical bars represent ± one standard error and each value is the mean of five replicates.

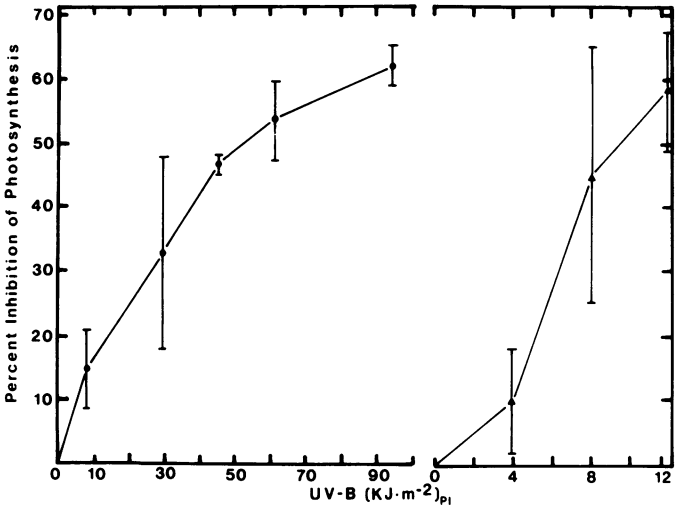

FIG. 5. Per cent inhibition of photosynthesis in *S. filiforme* by UV-B and the effect of PAR irradiance on UV-B-induced photosynthetic inhibition. Dose rates for UV-B irradiation in the absence of PAR (●——●) ranged from 0.37 to 1.3 $w \cdot m^{-2}_{PI}$. Dose rates for UV-B irradiation in the presence of 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR (▲——▲) ranged from 0.46 to 1.0 $w \cdot m^{-2}_{PI}$. Zero % inhibition averaged 40.4 ± 10.6 μmol $CO_2 \cdot mg\ Chl^{-1} \cdot h^{-1}$. Vertical bars represent ± one standard error and each value is the mean of 10 replicates.

mine optimal conditions for photosynthesis by the seagrasses. Leaf tissue was equilibrated at the above conditions in 20 ml FSSW for 10 min and then transferred to 5 ml fresh FSSW containing 15 μl [^{14}C]bicarbonate (1 $mCi \cdot ml^{-1}$, 50 $mCi \cdot mM^{-1}$).

Following an incorporation period of 15 min, each sample was homogenized and successively extracted with host methanol and

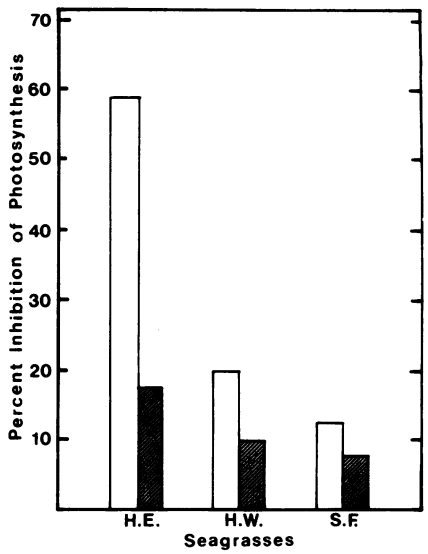

FIG. 6. Attenuation of photosynthetic inhibition of epiphytic shielding. Epiphytes present (▨), epiphytes removed (□). Results based on duplicate samples exposed to 0.94 $w \cdot m^{-2}_{PI}$, total dosage 20.4 $kJ \cdot m^{-2}_{PI}$. Average dry weight of epiphytic growth (mg epiphyte/g leaf tissue): *H. engelmannii*, 100.3 mg; *H. wrightii*, 22.2 mg; *S. filiforme*, 75.5 mg.

then with water. Chl was extracted from the methanol-water extract with ether. Total Chl was determined according to the method of Strain and Svec (33). Radioactivity in the methanol-water fraction was determined by adding a 0.1-ml aliquot to 10 ml Aquasol-2 (New England Nuclear) and counted in a Beckman LS 100-C scintillation counter. Photosynthetic rate was determined according to Goldman *et al.* (15). Inhibition of photosynthesis is expressed as the percentage decrease from the rate of ^{14}C uptake per unit Chl by the irradiation control plants (P_m) to values of uptake by the plant exposed to UV-B only (P_k); *i.e.*

$$\% \text{ Inhibition} = \frac{P_m - P_k}{P_m} \times 100$$

Per cent inhibition of photosynthesis was selected as the means of data analysis, rather than photosynthetic rate, to normalize the data; *i.e.* remove the independent and environmentally induced variation in photosynthetic rate and Chl content seen during the study.

In all photorepair studies, the dark control was used in place of the irradiation control for determining per cent inhibition of photosynthesis.

Epiphyte Studies. Leaf tissue subsamples of each seagrass were weighed with epiphytes intact and placed in Petri plates containing FSSW for UV-B irradiation. After irradiation, leaf tissues were quickly stripped of epiphytes, weighed, and their photosynthetic rates determined as previously described. These results were compared with the photosynthetic rates of tissues stripped of epiphytic growth prior to irradiation.

Scanning Electron Microscopy. Seagrass leaves were prepared for SEM by fixing in glutaraldehyde (2% v/v in FSSW, 20‰ salinity) overnight and postfixing in OsO_4 (2% v/v in FSSW, 20‰ salinity) for 2.5 h. Following dehydration in ethanol, the leaves were critically dried, coated with platinum-gold, and viewed in an ETEC Autoscan scanning electron microscope.

RESULTS

Sensitivity of Photosynthesis to UV-B. The intrinsic sensitivity of seagrass photosynthesis to UV-B was determined by exposing each species to increasing dose rates of UV-B. All applications of

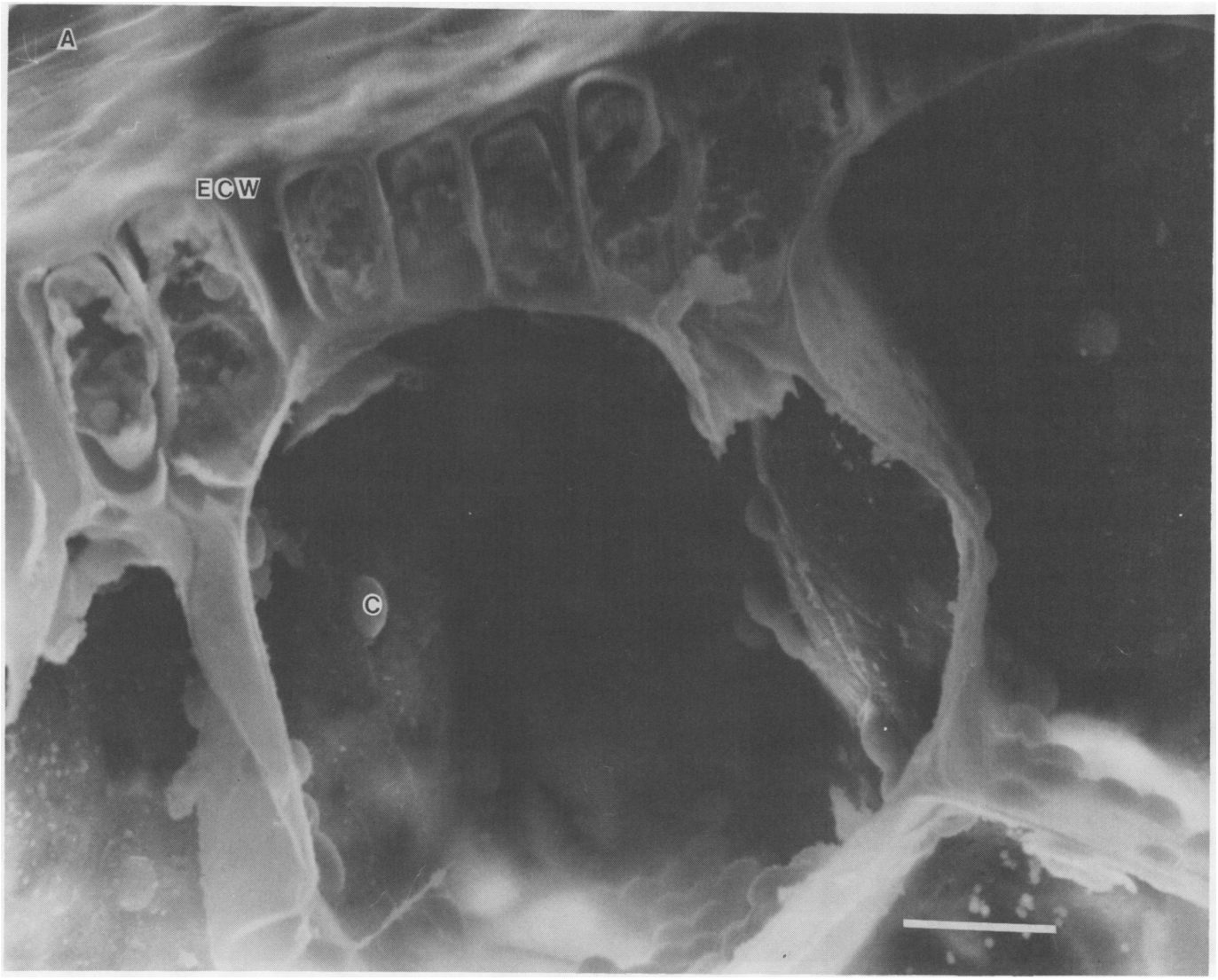

FIG. 7. Scanning electron microscopy of cross-section through seagrass leaves. A, *S. filiforme* (× 900); B, *H. wrightii* (× 1900); C, *H. engelmannii* (× 600). Epidermal cell walls (ECW); Mitochondria (M); Chloroplast (C). Bar represents 10 μm in all micrographs. Average cell wall thickness (leaf-water interface): *S. filiforme,* 1.5 ± 0.5 μm; *H. wrightii,* 1.0 ± 0.5 μm; *H. engelmannii,* 0.5 ± 0.2 μm. Values are the average of four sample sets.

UV-B to *Halophila* resulted in significant photosynthetic inhibition (Fig. 3). A linear relationship between UV-B dosage and per cent inhibition of photosynthesis was seen to approximate 14.7 kJ·m^{-2}_{PI}, or 50% photosynthetic inhibition. At the dose rates employed, UV-B dose rate had no statistically significant effect on photosynthetic inhibition. Total dosage of UV-B determined the extent of inhibition. Reciprocity was observed; *i.e.* at a given UV-B dosage, low dose rates over a long period of time produced the same degree of photosynthetic inhibition as higher dose rates over a shorter period. The maximum UV-B experienced by *Halophila* in the natural system is approximately 3.7 kJ·m^{-2}·day^{-1}_{PI} at dose rates approaching a maximum of 0.4 w·m^{-2}_{PI}. Simulation of these peak solar conditions with FS-40 sunlamps resulted in 10% inhibition of photosynthesis.

Unlike the effect of UV-B on *Halophila,* photosynthesis in *Halodule* is clearly influenced by the rate of UV-B exposure as well as the total amount applied (Fig. 4). Increasing either variable enhanced photosynthetic inhibition. Peak, ambient levels of UV-B seen at the mean leaf depth of *Halodule* in the natural system were 9.2 kJ·m^{-2}·day^{-1}_{PI} at 0.46 w·m^{-2}_{PI}. The FS-40 simulation of this irradiance resulted in less than 2% photosynthetic inhibition. Enhanced dose rates averaging 0.88 and 1.16 w·m^{-2}_{PI} UV-B (Fig. 4) increased photosynthetic inhibition to 3 and 15%, respectively, at the ambient total dosage of 9.2 kJ·m^{-2}_{PI}.

Syringodium required prolonged UV-B irradiation (55.0 kJ·m^{-2}_{PI}) to induce 50% photosynthetic inhibition (Fig. 5); approximately 4 times the dosage required to cause the same level of inhibition in *Halophila.* However, as in *Halophila,* reciprocity of dose rates at a given dosage was seen in *Syringodium.* The degree of inhibition observed was a function of the total UV-B dosage applied. The rapid, initial increase in photosynthetic inhibition at UV-B dosages reflecting peak natural conditions for *Syringodium* (7.35 kJ·m^{-2}·day^{-1}_{PI}) indicated a low intrinsic tolerance to UV-B.

During irradiation studies involving high dosages and/or dose rates of UV-B, an interesting observation was made with respect to the coloration of the methanol-water fraction. In all controls (dark and irradiation) and short term UV-B treatments, the methanol-water fraction was characteristically clear. However, after long term exposure to UV-B, the methanol-water fraction from *Halophila* appeared to accumulate a red pigment. Also, yellow methanol-water fractions were obtained from Chl extractions of *Halodule* and *Syringodium* which experienced irradiation periods of long duration. Although not specifically measured, these data

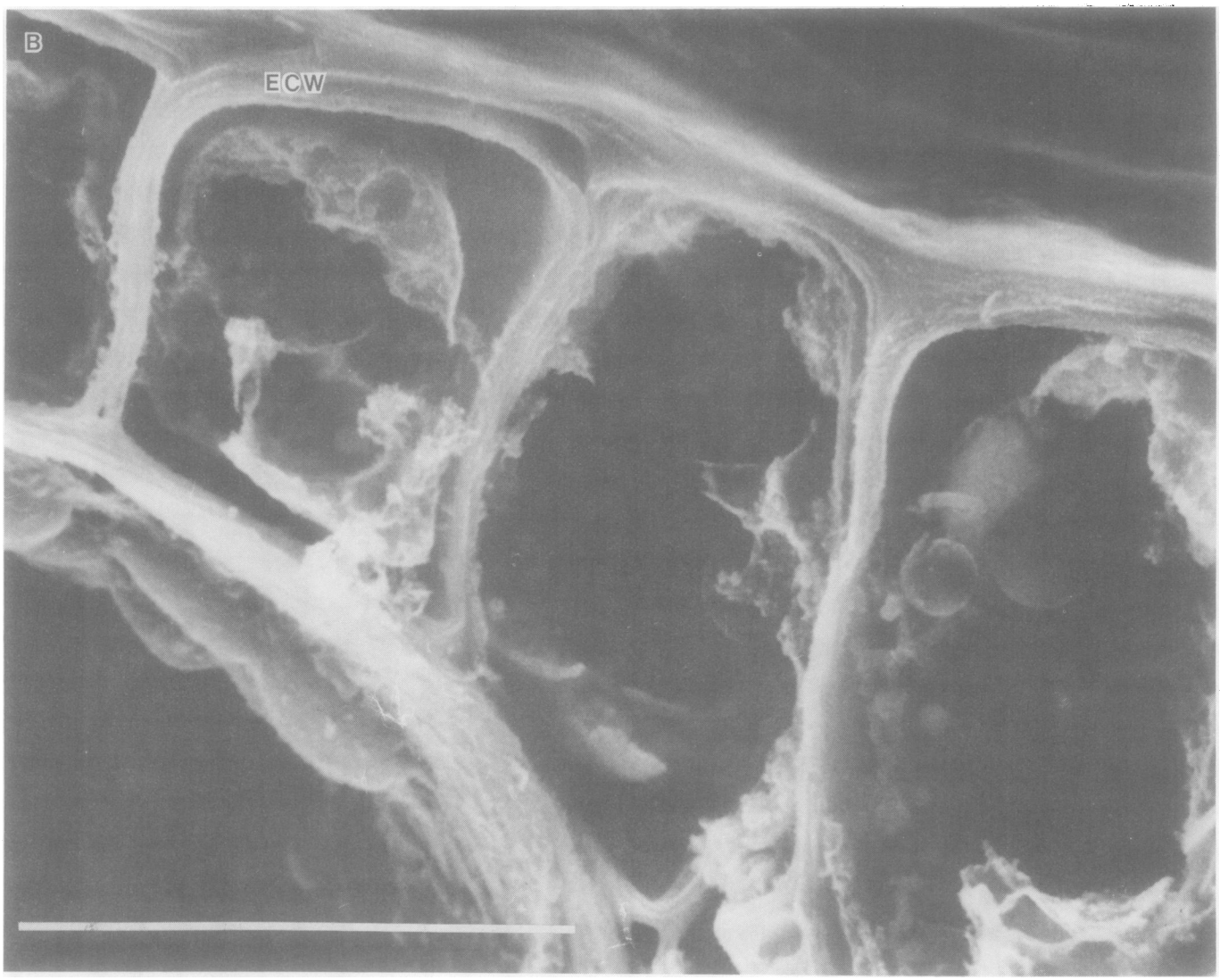

FIG. 7B

suggest the possibility of synthesis of anthocyanin of other flavonoids in response to UV-B irradiation.

Photorepair Studies. The possibility of UV-B-induced, photosynthetic inhibition being subject to photorepair was examined in each of the seagrasses. In these experiments, where 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR was combined with UV-B, *Halophila* failed to show a signficant photorepair response (Fig. 3). Statistically, the presence of a photorepair mechanism is doubtful, however, a slight and general reduction in the mean value of photosynthetic inhibition was obtained. No correlation between UV-B dose rate and photorepair efficiency was observed (Fig. 3).

No photorepair capability dealing with UV-B was apparent in *Syringodium.* The combined effect of 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR and UV-B irradiation seemed to increase this species' sensitivity to UV-B (Fig. 5). The increase in photosynthetic inhibition observed was not due to photooxidation by PAR; preliminary studies to determine the optimum photosynthetic PAR intensity eliminated this possibility. The photosensitization response was obtained with all UV-B dose rates applied. Fifty % photosynthetic inhibition was reached at only 10.0 $kJ \cdot m^{-2}_{PI}$, one-fifth the dosage required to produce the same inhibition by UV-B irradiation alone. This photosensitization is the subject of a paper in preparation.

Halodule was the only species to give clear evidence of a photorepair mechanism able to reverse or attenuate UV-B-induced photosynthetic inhibition (Fig. 4). The addition of PAR to the irradiation regime held the level of inhibition to approximately 10% regardless of UV-B dose or dose rate supplied. The data indicate a photosensitization by PAR when low UV-B dose rates are applied, a response similar to that in *Syringodium.* This photosensitization makes the apparent reciprocity of the photorepair response (in terms of UV-B dosage) suspect; *i.e.* photosensitization may be masking photorepair. This attenuation of photosynthetic inhibition remained relatively constant up to 20.0 $kJ \cdot m^{-2}_{PI}$, twice the maximum ambient dosage seen by this species in the natural system.

Epiphyte Studies. The attenuation of UV-B by epiphytic growth on leaf surfaces was found to reduce photosynthetic inhibition in the underlying tissues. An example of the results representing an epiphytic bloom is seen in Figure 6. The presence of thick epiphytic layers on leaf surfaces significantly reduced the degree of photosynthetic inhibition in comparison to denuded tissues. The shielding effect on undamaged tissues of each species appeared to correspond well to dry weights of epiphytes present during blooms. The explosive appearance and disappearance of epiphytic blooms, cold-cropping and other physical damage received by mature, epiphyte-bearing tissues due to the environment prevented sample acquisition across the range of epiphytic population sizes required for reliable statistical analysis.

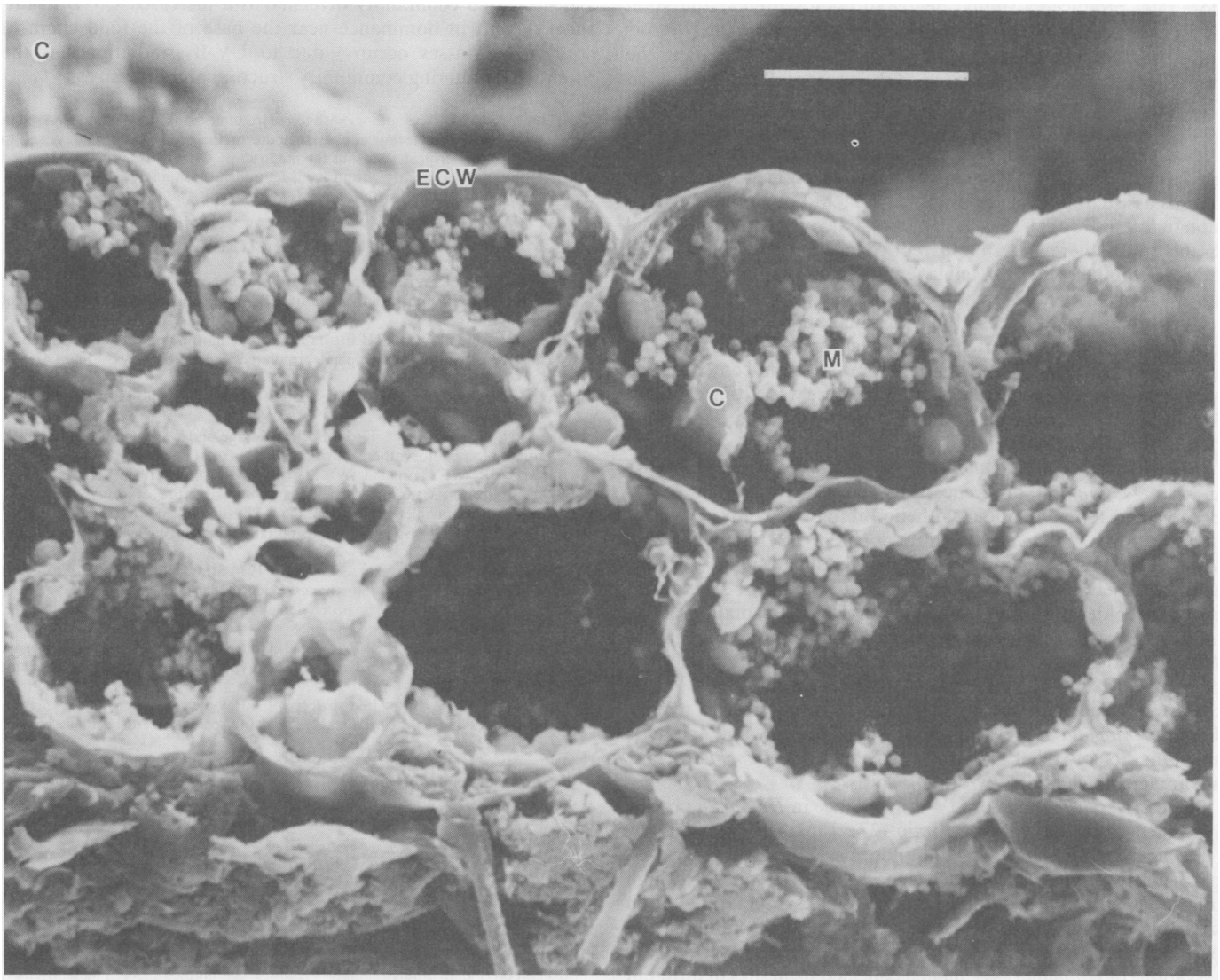

FIG. 7C

Scanning Electron Micrographs. Examination of electron micrographs of the three aquatic angiosperms provided useful information concerning their photosynthetic sensitivity to UV-B. The epidermal cell layer of *Syringodium* was shown to be composed of many small, thick walled cells (Fig. 7A). The blade of *Halodule* appears to possess less epidermal thickening. The cells of the epidermis are larger and less thickly walled (Fig. 7B). The photorepair abilities in this species seem quite effective in dealing with the UV-B transmission which occurs. Scanning electron micrographs of *Halophila*, the most sensitive of the seagrasses to UV-B-induced photosynthetic inhibition, show the leaf to be only two to three cells thick (Fig. 7C). These cells are large and very thin walled in comparison to *Halodule* and *Syringodium* and may be a significant factor responsible for *Halophila*'s high sensitivity to UV-B.

DISCUSSION

None of the seagrasses examined in this study were totally insensitive to UV-B. Although *Halodule* was able to tolerate ambient levels of UV-B, higher dose rates and dosages (used to simulate atmospheric ozone reduction) were inhibitory. The sensitivity of *Halodule* to UV-B appears to be more a function of UV-B dose rate than the total UV-B dose. The limit of effective physiological resistance (the dose rate above which photosynthetic inhibition increases with UV-B dose) appears to be a dose rate of 0.9 $w \cdot m^{-2}_{PI}$ (Fig. 4). This dose rate reflects ambient conditions at the air/water interface in the natural system. *Halodule* has the capacity to endure at least a doubling of the ambient UV-B at mean blade depth before 10% photosynthetic inhibition is observed.

Evidence of a photorepair mechanism effective in dealing with UV-B-induced photosynthetic inhibition was seen only in *Halodule*, supporting the suggestion of photoreactivation by Van Baalen (36) in his work with *Agmenellum quadruplicatum* (a blue-green alga). Such a mechanism is of great value to *Halodule* as it receives the most intense and continuous exposure to UV-B of the seagrasses in the system. Because of its physiological tolerance and photorepair capabilities, *Halodule* has the greatest potential of the seagrasses tested to withstand enhanced levels of UV-B. Fox and Caldwell (13) has shown UV-B to accentuate interspecific competition between coexisting species. Dominance in the system is shared by *Halodule* and *Syringodium* in terms of both abundance and biomass. In a UV-B-stressed environment, *Halodule* possesses the advantage over *Syringodium*.

Large dosages of UV-B were required to induce severe photosynthetic inhibition in *Syringodium* (Fig. 5). However, this species was less tolerant of ambient UV-B levels than *Halodule*. No evidence of photochemical resistance to UV-B was observed, all

dose rates produced a similar degree of photosynthetic inhibition at a given dosage. *Syringodium* apparently relies primarily on its thick epidermal cell layer to reduce penetration of UV-B to the more sensitive mesophyll tissue. The work of Robberecht and Caldwell (28) on terrestrial angiosperms has shown epidermal transmission of UV-B to be generally less than 10%. Principally, the attenuation was due to the structural components of the epidermis, although flavonoids and related pigments in the epidermis assisted in the screening of UV-B. Although the transmission of UV-B through seagrass epidermal layers was not measured in this study, there was an apparent correlation between cell wall thickness of the epidermal cell layer and photosynthetic sensitivity to UV-B by *Syringodium* and *Halophila* (Fig. 7).

Biosynthesis of UV-absorbing pigments in response to UV-B irradiation has been reported by Caldwell (6), Wellman (38), and Lindoo and Caldwell (22). Although the flavonoid content of the seagrasses was not specifically examined there was strong evidence for anthocyanin or flavonoid-like pigment production after long periods of UV-B irradiation.

Photosynthesis in *Halophila* was the most sensitive to UV-B. As in *Syringodium,* no difference between UV-B dose rates was observed in terms of photosynthetic inhibition. Unlike *Syringodium* however, *Halophila* has little apparent morphological protection. It is possible that the major difference in photosynthetic sensitivity between *Syringodium* and *Halophila* may be the differences in epidermal tissue. Increases in UV-B irradiation above ambient conditions were proportionally far more detrimental to *Halophila* than either *Syringodium* or *Halodule.* This species appears to rely on the environment to shield it from UV-B. Where depth or turbidity of the water column is insufficient to remove UV-B, *Halophila* is able to profit from detrital and epiphytic shielding. Its low relief growth-form also allows *Halophila* to take advantage of "shading" by other seagrasses.

A possible mechanism of UV-B avoidance in *Halophila* may be suggested from the work of Virgin (37), Lipkin (23), and Drew (12). These studies have shown chloroplasts of some seagrasses, particularly *Halophila stipulacea,* to clump in response to high intensities of visible radiation reducing photosynthetic inhibition from photooxidation. Leaf tissues exhibiting such clumping appear pale but are not photosynthetically inhibited (12). Our observations of *Halophila engelmannii* collected from sites of different characteristic PAR intensities indicate the clumping response may be present in this species. As high PAR intensities usually corresponded to high UV-B dose rates (up to the ambient maximum), chloroplast clumping due to PAR may also serve to reduce in part the effective UV-B dosage. This response may be responsible for the slight, but general reduction in photosynthetic inhibition when UV-B irradiation was combined with 700 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR (Fig. 3).

Epiphytic growth is common to all three seagrasses, and each benefits to some degree from it as a shield from UV-B. This shielding is of greatest importance to *Halophila* because of its extreme sensitivity to UV-B. The range of this species in a very shallow water environment (such as the natural system examined here) may be influenced by the boom and burst cycles exhibited by epiphytes. *Halodule* and *Syringodium* often take on a cattail-like appearance at the height of epiphytic blooms, which may be of particular value as the leaves approach the air/water interface. A partial listing of epiphytic species common to these seagrasses is provided by Harlin (18).

In the event of increasing ambient levels of UV-B, *Halophila* would most likely be the first seagrass to be removed from the system, displaced by the migration of *Halodule* and *Syringodium* to greater depths. These species in turn may become stunted and less abundant as UV-B intensities increase relative to PAR levels. The diversity of the system may suffer accordingly. Worrest *et al.* (30) using an artificial estuarine system have seen reduced biomass and decreased community diversity with increased UV-B irradiance. A shift in dominance near the base of the food chain (a position seagrasses occupy) due to UV-B irradiation has the potential for altering community structure and diversity.

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